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RESEARCH PAPER

Assessment of transpiration efficiency in peanut (*arachis hypogaea* l.) under drought using a lysimeter system

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Keywords

Arachis hypogaea; drought tolerance; lysimeter; peanut; transpiration efficiency.

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ABSTRACT

Transpiration efficiency (TE) is an important trait for drought tolerance in peanut (*Arachis hypogaea* L.). The variation in TE was assessed gravimetrically using a long time interval in nine peanut genotypes (Chico, ICGS 44, ICGV 00350, ICGV 86015, ICGV 86031, ICGV 91114, JL 24, TAG 24 and TMV 2) grown in lysimeters under well-watered or drought conditions. Transpiration was measured by regularly weighing the lysimeters, in which the soil surface was mulched with a 2-cm layer of polythene beads. TE in the nine genotypes used varied from 1.4 to 2.9 g kg^{-1} under well-watered and 1.7 to 2.9 g kg^{-1} under drought conditions, showing consistent variation in TE among genotypes. A higher TE was found in ICGV 86031 in both well-watered and drought conditions and lower TE was found in TAG-24 under both water regimes. Although total water extraction differed little across genotypes, the pattern of water extraction from the soil profile varied among genotypes. High water extraction within 24 days following stress imposition was negatively related to pod yield (r^2 = 0.36), and negatively related to water extraction during a subsequent period of 32 days (r^2 = 0.74). By contrast, the latter, *i.e.* water extraction during a period corresponding to grain filling (24 to 56 days after flowering) was positively related to pod yield (r^2 = 0.36). TE was positively correlated with pod weight (r^2 = 0.30) under drought condition. Our data show that under an intermittent drought regime, TE and water extraction from the soil profile during a period corresponding to pod filling were the most important components.

INTRODUCTION

Transpiration efficiency (TE, g biomass kg^{-1} water transpired) is an important component of water-use efficiency (WUE, in kg grain mm^{-1} water) and a major source of yield variation under drought stress in many crops. It is difficult to assess TE gravimetrically by measuring biomass increase and related transpiration over a significant length of time because of problems in maintaining plants in pots for long periods while monitoring their water use and keeping soil evaporation to a minimum. It is even more difficult to assess TE under field conditions, especially for separating the two components of evapotranspiration. Relating TE to yield parameters from field-based experiments combines both problems described above, although a method has been designed (Cooper *et al.* 1983). To address these limitations, a lysimetric system, *i.e.* a system of long and large PVC tubes filled with soil, which mimics field conditions as closely as possible, has been developed at ICRISAT (Vadez *et al.* 2008). This system allows assessment of TE over long periods, together with estimation of yield. In addition, it allows dynamic measurement of water extraction from the soil profile, which can be related to yield of the plants assessed. Hence, the system allows simultaneous assessment of three components of yield – transpiration, transpiration efficiency and harvest index – as defined by Passioura (1977).

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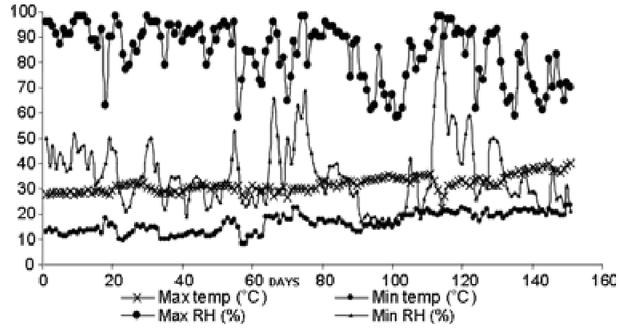
Peanut (*Arachis hypogaea* L.) is an important oilseed, food legume and cash crop grown mainly under rainfed conditions in the semiarid tropics (SAT) throughout the world. The major constraint for peanut crop productivity in rainfed areas is often erratic and unpredictable rainfall patterns. TE has long been used as a major characteristic to improve yield under intermittent drought conditions (Turner 1986; Wright *et al.* 1994). TE improvement has been achieved in breeding of crops such as wheat (Condon *et al.* 2002; Rebetke *et al.* 2002), groundnut (Hebber *et al.* 1994; Krishnamurthy *et al.* 2007) and cowpea (Ismael & Hall 1992), and breeding efforts have been made to include TE in the improved germplasm (Udaykumar *et al.* 1998).

In previous work, we attempted to quantify TE directly (Bhatnagar-Mathur *et al.* 2007; Krishnamurthy *et al.* 2007) using the ratio of biomass accumulated over a substantial period (2 to 4 weeks) divided by total transpiration during that period. Here, we report on efforts to quantify the genetic variation available for TE, measured over longer periods between flowering and maturity, using a lysimetric system consisting of long and large PVC tubes mimicking a real soil profile. We used a novel experimental setup that allows simultaneously assessment of TE and yield to test the hypothesis that TE will be related to yield under water stressed conditions, by assessing the relationship between yield and TE under different watering regimes. In addition, we hypothesised that water uptake at critical times during plant growth is important, as previously suggested (Vadez *et al.* 2007). These hypotheses were assessed by examining several peanut genotypes, differences in their patterns of water extraction from the tubes over time and relationships between water extraction at different times and pod yield under intermittent drought stress.

MATERIALS AND METHODS

This experiment was conducted at ICRISAT (Patancheru, India) during the winter season (20 December 2007 to April 2008) using lysimeters (PVC cylinders 1-m long, 20-cm diameter) and a fully automated rain-out shelter (25-m long, 25-m wide, 11-m high at the centre and 8-m high at both sides) to protect the plants from rainfall. During the crop growing season maximum and minimum temperature was 36 °C and 16 °C and maximum and minimum relative humidity was 84% and 35%, respectively (Fig. 1). Nine groundnut genotypes (Chico, ICG S 44, ICGV 00350, ICGV 86015, ICGV 86031, ICGV 91114, JL 24, TAG 24 and TMV 2) were sown in the lysimeters. The diameter of the tubes was determined so that the surface area available to each plant in a tube corresponded to the area available under field conditions at a sowing density of approximately 30 plants/m^2 (Vadez *et al.* 2008). The depth of the tubes was based on an estimation of rooting depth of groundnut in this type of soil (Alfisol).

The lysimeters contained Alfisol collected from the ICRISAT farm that was dried and sieved to remove large



1 **Fig. 1.** Local weather at ICRISAT during the crop growth period (from 2 December 2007 to 30 April 2008), with daily minimum (recorded at 7:17 IST) and maximum (recorded at 14:1r IST) temperature (°C) and relative humidity (%).

soil aggregates, and amended with single super phosphate and muriated potash at a rate of 200 mg kg^{-1} soil. Lysimeters were filled with approximately 50 kg soil, in two 20-kg increments, each of these saturated with water (20% w/w) immediately after filling to allow time for the water to percolate through the soil before proceeding with the next soil increment, and a final increment of 10 kg that was also watered to field capacity. No packing of the soil was undertaken, and further soil was added until the soil surface was approximately 5 cm from the top of the tube. The overall bulk density across tubes was homogenous and close to 1.4. The top 3 cm of soil contained 2 g carbofuran to prevent damage from soil-borne pests. All lysimeters were inoculated with *Rhizobium* strain NC-29 (IC 7001) using a liquid inoculation method (Brockwell 1982) to ensure better plant nodulation. The soil surface of the cylinders was mulched with a 2-cm thick layer of polythene beads. Previous assessments (data not shown) indicated that this mulching controlled over 90% of soil evaporation and therefore, tube weight differences were considered to reflect plant water uptake for transpiration.

Seeds were sprayed with 90% Etherel solution and air-dried to break dormancy, if necessary. At planting, soil was wetted and seeds planted at a rate of two per cylinder and later thinned to one plant per cylinder. Fifteen cylinders per each of the nine genotypes were planted. The experiment used a randomized block design (RBD) with five replications and three sets of plants per treatment. After sowing, watering was done at regular intervals and all three sets of plants were treated equally until flowering. At flowering, each set of plants was treated differently: one set was harvested to assess biomass and leaf area at the time of imposing the treatment, one set was used as a well-watered treatment (WW), and the other set was used as a drought-stress treatment (DS), with five replications per genotype and treatment. All lysimeters in the WW and DS treatments were optimally irrigated to 90% of field capacity at flowering, *i.e.* the tubes were allowed to drain over a period of 40 h. After which, an intermittent stress was imposed by partially re-watering the DS tubes on different dates with 1 l (twice a week, 500 ml per application) of water at 28, 35, 42, 50 and 57 days after the last full irrigation (38 DAS). Such intermittent stress is typically encountered by groundnut in the field under rainfed conditions. Transpiration was measured by regular weighing of the lysimeters (twice per week). Previous assessments (data not shown) indicated that mulching controlled over 90% of soil evaporation and therefore, tube weight differences were considered to reflect plant water uptake for transpiration.

TE was calculated as:

$$TE = (DM2 - DM1)/(W2 - W1) + WA$$

where DM1: mean shoot biomass in a set of pots harvested 4weeks after sowing; DM2: shoot biomass at harvest; W1: weight of the lysimeter at the time of adding mulching beads; W2: weight of the lysimeter at time of final harvest; WA: water added to individual cylinders after regular weighing.

Plants were harvested at 130 DAS, and separated into leaf, stem and pod fractions. Leaf area was measured only in well-watered plants. Dry weights of stem, leaf and pod were measured after drying at 80°C in a hot air oven for 48 to 72 h.

Statistical analysis

Data were analysed using residual maximum likelihood (ReML) analysis and simple ANOVA. Correlations between traits were estimated using the statistical analytical program SAS version 9.0.

RESULTS

Water uptake during stress

There were significant variations among genotypes in total water uptake from the tubes from the time of stress imposition until harvest. Average total water uptake across genotypes under drought stress (6404 g) was lower than under well-watered conditions (13905 g). Water uptake varied substantially between genotypes during the intermittent stress and ranged from 5990 g plant^{-1} in ICGV 86015 to 6862 g plant^{-1} in ICGV 91114. Under WW conditions, water use ranged between 9290 g plant^{-1} in TAG 24 and 16370 g plant^{-1} in ICGV 00350 (Table 1). There was no significant relationship between water uptake under WW conditions and water uptake under DS conditions. For instance, while TAG 24 had the lowest water uptake under WW conditions, it had among the highest water uptake under DS conditions.

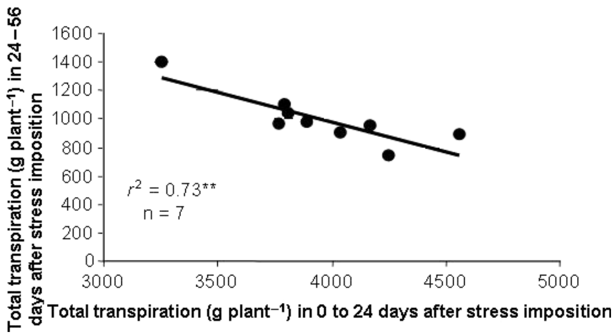
Besides measuring volumes of water taken up during the entire crop cycle, we also measured water uptake at regular intervals by weighing the cylinders, following the hypothesis that water uptake at key times may be important. During the initial 24 days after irrigation was withheld, genotypes TMV 2 and ICGV91114 took up more water than Chico (Table 1). This period corresponded approximately to the duration of flowering in these lines. By contrast, from 24 to 56 days after stress imposition, Chico took up more water than TMV 2, ICGV 00350, ICGV 91114 or JL 24, and TAG 24 had the second highest water uptake. This period corresponds to pod development and filling. Fig. 2 clearly shows that water uptake in the 24 days following stress imposition was significantly negatively related to water uptake in the 24–56-day period following stress impositions (r^2 = 0.74).

Relation between water uptake and leaf area

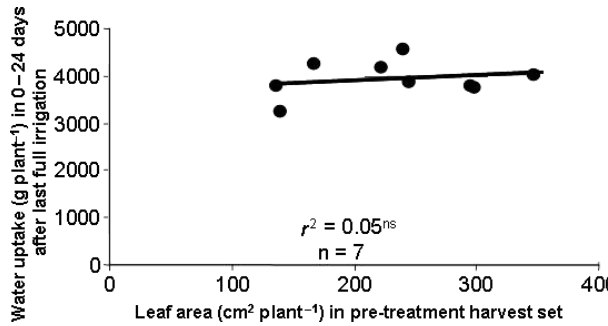
One possible cause of the differences in water uptake under DS conditions could be differences in initial leaf area when the last full irrigation was applied. Leaf area was measured on a set of identical plants (pre-harvested), which were harvested before imposing the stress, and no significant relationship (r^2 = 0.04; Fig. 3) was found with water uptake in either initial harvest or in plants 24 days following the last full irrigation. Genotypes Chico and

Table 1. Total transpiration (Tr) in g plant^{-1} at different stages of reproduction and pod filling in nine peanut genotypes under drought stress (DS) or well-watered (WW) conditions. Data are mean values of five replicate plants (n = 5), each plant growing in an individual PVC lysimeter tube. Least significant differences (LSD) of means are at 5% level and df is 36.

	Total Tr (total water extracted)		Total Tr (0–24 days after stress imposition)		Total Tr (24–56 days after stress imposition)		Total Tr (57–69 days after stress imposition)	
Genotype	DS	WW	DS	WW	DS	WW	DS	WW
Chico	6288	11470	3250	3640	1850	4580	550	2830
ICGS 44	6817	13300	4167	4290	1417	5430	500	3160
ICGV 00350	6338	16370	4038	3980	1250	7490	462	4440
ICGV 86015	5990	15100	3770	4010	1460	6170	430	4420
ICGV 86031	6480	14426	3810	3306	1620	5380	580	5310
ICGV 91114	6862	14890	4562	5050	1288	6170	612	3190
JL 24	6225	14280	3888	4430	1250	5050	575	4290
TAG 24	6510	9290	3790	3080	1730	3810	560	2020
TMV 2	6130	16020	4250	4980	1040	6770	430	3720
Grand mean	6404	13905	3947	4085	1434	5650	522.0	3709
LSD	808.1	3953.9	755.0	1353	380.8	1799	205.3	2593



2 **Fig. 2.** Significant relationships for total transpiration (g plant^{-1}) at different stages of crop development. Significant negative relationship between water uptake at 0 to 24 days and that at 24 to 56 days following stress imposition in nine peanut genotypes. Each data point represents mean (n = 5) of each genotype.



3 **Fig. 3.** Lack of a clear relationship between pre-treatment leaf area (cm^2 plant^{-1}) and water uptake (g plant^{-1}) during a 24-day period after withdrawal of irrigation in nine peanut genotypes. Each data point represents mean (n = 5) of each genotype.

TAG 24 had the lowest leaf area, whereas ICGV 00350 and ICGV 86031 had the highest leaf area pre-harvest in well-watered plants (Table 2).

Dry weight at harvest and TE among genotypes

At the time of harvest, aerial biomass of DS plants across the genotypes was only slightly lower (13.59 g plant^{-1}) than that in WW conditions (16.80 g plant^{-1}), and this was likely related to higher remobilization of water towards pods under WW conditions. Aerial dry biomass varied significantly under DS conditions, and was lowest (9.54 g) in TAG 24 and highest (17.32 g) in ICGV 86031. Similarly, biomass varied under WW conditions, and TAG 24 still had the lowest biomass (22.19 g) (Table 2).

Pod weight decreased under DS conditions compared to WW, from a mean across genotypes of 3.79 g pod DW plant^{-1} to a mean of 16.11 g pod DW plant^{-1} under WW, indicating that plants underwent very severe intermittent stress. Under drought stress, ICGV 86031 and Chico had the highest pod yield, both above 5 g plant^{-1}, whereas JL 24 and ICGV 91114 had the lowest pod yield, below 3 g plant^{-1}. Under WW conditions, TMV 2 and JL 24 had the highest pod yields, whereas TAG-24 had the lowest (Table 2).

Transpiration efficiency across the nine genotypes varied little between well-WW and DS conditions, being, respectively, 2.34 and 2.17 g kg^{-1} water transpired across genotypes (Table 2). However, TE varied from 1.79 to 2.91 g kg^{-1} under both WW and DS conditions. There was a consistent variation in TE among the nine genotypes. TE measured under WW conditions was relatively

Table 2. Leaf, shoot, pod, total dry matter (DW, g plant^{-1}) and transpiration efficiency (g biomass kg^{-1} water transpired) of nine peanut genotypes under drought stress (DS) or well-watered (WW) conditions. Data are mean values of five replicate plants (n = 5), each plant growing in an individual PVC tube..

	Leaf area (cm^2 plant^{-1})	Leaf DW (g plant^{-1})		Shoot DW (g plant^{-1})		Pod DW (g plant^{-1})		Total DW (g plant^{-1})		TE (g biomass kg^{-1} water transpired)	
Genotype	Pre-harvest	Pre-harvest	WW (final harvest)	DS	WW	DS	WW	DS	WW	DS	WW
Chico	138.8	1.59	5.15	12.10	5.40	5.30	18.93	16.07	23.15	2.19	1.82
ICGS 44	221.7	2.55	8.70	12.31	9.16	3.27	17.12	15.58	34.98	1.79	2.75
ICGV 00350	345.9	3.22	7.00	15.63	11.40	3.48	18.12	19.11	32.90	2.28	2.09
ICGV 86015	297.5	3.24	7.14	12.39	7.12	4.79	14.61	16.22	24.81	1.80	1.68
ICGV 86031	295.1	3.11	9.96	17.32	12.23	5.53	14.78	22.85	36.97	2.91	2.91
ICGV 91114	239.1	2.20	8.20	12.31	9.64	2.89	11.57	15.19	29.40	1.80	1.96
JL 24	244.5	2.55	10.21	16.84	11.54	1.26	21.55	18.10	43.31	2.34	2.87
TAG 24	135.3	1.67	4.55	9.54	4.20	4.48	6.12	14.02	14.80	1.90	1.47
TMV 2	166.4	1.66	6.73	13.91	9.80	3.13	17.55	17.04	34.08	2.48	2.25
df	36	36	36	36	36	36	36	36	36	36	36
SE	30.45	0.262	1.846	1.741	1.405	1.755	4.097	2.362	7.294	0.384	0.4781
P value	0.001	0.001	0.064	0.002	0.001	0.265	0.034	0.025	0.088	0.062	0.024

well related to TE under DS conditions ($r^2 = 0.31$; Fig. 4). Higher TE was found in ICGV 86031 in both WW and DS conditions and lowest TE was in TAG-24 under WW and ICGS 44 under DS conditions (Table 2). Genotype ICGV 86015 also had a consistently low TE across both water regimes. Compared to WW conditions, TE increased under DS in all genotypes except ICGV 91114, ICGS 44 and JL 24.

Pod yield and relationship with water uptake and TE

A general assumption on the role of rooting traits is that larger and more roots contribute to higher water uptake, itself contributing to higher yield. Here, we did find this general trend when plotting water uptake data from WW and DS plants against pod yield (Fig. 5); however, within each treatment, the trends differed. While it remained true that higher water uptake was significantly related to higher pod yield under WW conditions ($r^2 = 0.34$), there was no significant relationship between water uptake and pod yield under DS conditions ($r^2 = 0.01$) (Fig. 5). We pursued the analysis by assessing relationships between pod weight and water uptake at different times after imposition of stress. Pod weight was significantly and negatively correlated ($r^2 = 0.33$) with the water uptake during the 24 days following stress imposition, indicating that genotypes taking large amounts of water during that period ended with lower pod yields. By contrast, pod yield was positively and significantly correlated ($r^2 = 0.36$) with water uptake in the period between 24 and 56 days after imposition of stress, which corresponded to the period of pod development (Fig. 6). It was also interesting to note that the amounts of water taken up between 24 and 56 days after stress imposition was about two-times lower than the range of water uptake in the 24 days following stress imposition. Pod weight under DS conditions was also positively correlated with TE ($r^2 = 0.31$). A strong significant positive correlation ($r^2 = 0.64$) was also found between TE and pod weight under WW conditions (Fig. 7).

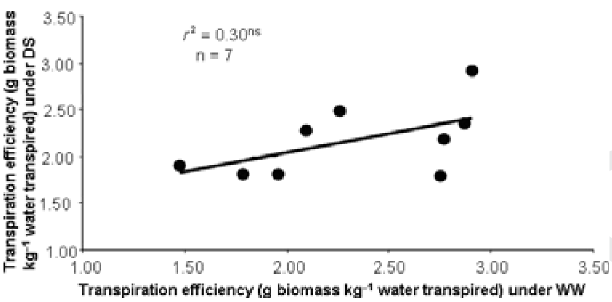


Fig. 4. Relationship between transpiration efficiency (TE, g biomass kg^{-1} water transpired) under well-watered (WW) and under drought stress (DS) conditions. Each data point represents mean (n = 5) of each genotype.

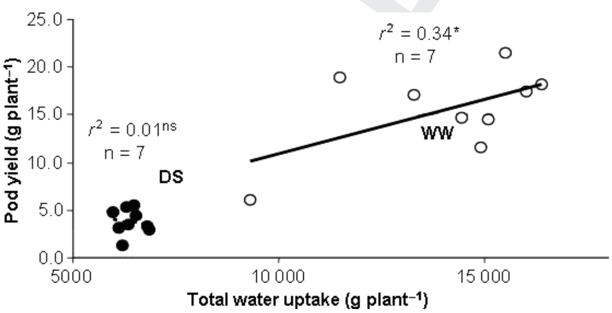


Fig. 5. Relationship between total water uptake (g $plant^{-1}$) and pod yield (g $plant^{-1}$) under drought stress (DS, filled black circles) and under well-watered (WW, open circles) conditions. Under DS, the relationship was negative, while under WW, the relationship was positive. Each data point represents mean (n = 5) of each genotype under different treatments.

DISCUSSION

The results of the present study show that groundnut plants grown in lysimeters and exposed to intermittent water stress from flowering onwards had very distinct patterns of water uptake, and such patterns had direct consequences for pod yield under intermittent water stress conditions. The total volume of water uptake had no relationship to pod yield under DS, whereas water uptake during pod filling was critical for achieving higher pod yields. Water uptake was not the only component contributing to higher pod yield, and TE under both DS and WW conditions had a significant positive association with pod yield.

Higher water uptake in the 24 days after stress imposition led to less water uptake in the subsequent 32 days and was directly related to lower pod yield. This was the case for genotypes TMV 2, ICGS 44 and ICGV 91114, which maintained high transpiration rates during the 24 days following stress imposition, but appeared to run

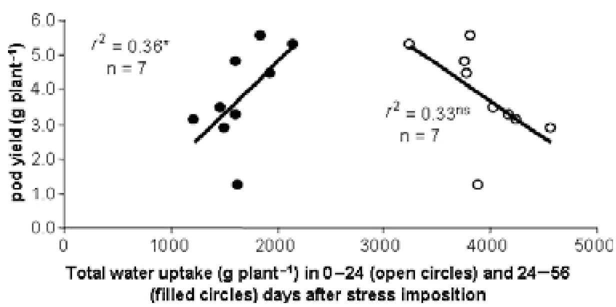


Fig. 6. Significant negative relationship between pod yield (g $plant^{-1}$) and total water uptake during the 0–24-day (open circles) period after stress imposition and significant positive relationship between pod yield (g $plant^{-1}$) and total water uptake during days 24–56 (black circles) after stress imposition. Each data point represents mean (n = 5) of each genotype of peanut.

LOW RESOLUTION FIG

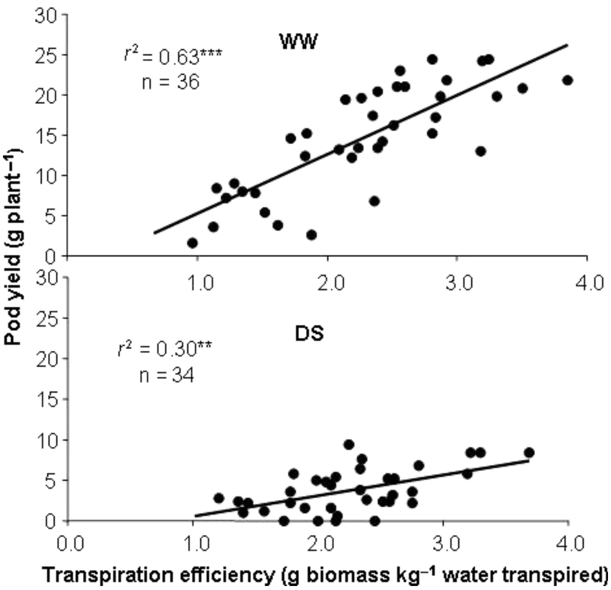


Fig. 7. Relationship between transpiration efficiency (g biomass kg^{-1} water transpired) and pod yield (g $plant^{-1}$) under well-watered (WW, top) and drought stress (DS, bottom) conditions in nine peanut genotypes. Each data point represents a replicated cylinder with one plant per cylinder.

short of water during later stages, from 24–56 days, after withdrawal of irrigation. By contrast, a more 'conservative' use of soil water, with lower amounts taken during the flowering period and larger amount during the pod filling period, was well related to the pod yield differences found. This was the case for genotypes Chico, TAG 24 and ICGV 86031. These data agree well with Meisner & Karnok (1992), who argue that sufficient water uptake at key times, *i.e.* reproductive stage and pod filling stage, during plant development is more important than across the whole growth cycle. In an earlier review, Vadez *et al.* (2008) hypothesised that better water uptake by roots at key stages, like pod filling, could be related to sparing use of water by shoots at initial stages when the soil is wet. This behaviour would permit saving water in the soil profile and leave water available for later stages during reproduction or pod filling. Nevertheless, our data show very clearly that large water uptake was not the critical factor in pod yield. We found that water uptake 24 to 56 days after stress imposition was the most critical parameter, where water uptake values ranged from 1220 to 2150 g, *i.e.* average of 38 to 67 g water per day, showing that small but critical amounts of water were needed, above a threshold value of 40 to 60 g.

The TE measurements agreed well with previous assessments (Krishnamurthy *et al.* 2007), where TAG 24 had low TE and ICGV86031 had high TE, in accordance with previous data. These results indicate the validity of previous TE assessments using smaller pots. In addition, we found that TE measured under DS was significantly related to TE measured under WW conditions, in agreement with previous work (Wright *et al.* 1994; Nageswara Rao *et al.* 1993; Udayakumar *et al.* 1998). These data indicate that TE is a highly relevant trait for crop improvement in groundnut and that, to a certain extent, TE screening can be done either under WW or DS conditions.

Here, when intermittent drought stress was imposed, TE contributed over 30% to pod yield variations, even under WW conditions The positive association between TE and pod yield under WW conditions is in contrast to previous results that higher TE is related to poorer plant performance under non-stressed conditions (Wright *et al.* 1991). If confirmed, the relationship with TE found here would indicate that there might be limited negative trade-off from breeding for higher TE. Under DS conditions, ICGV 86031 had a higher TE and also high pod yield, whereas it also had among the largest water uptakes during the critical 24–56-day period after stress imposition. Although TAG 24 had the lowest TE, it maintained a high pod yield, thanks to high water uptake during this key period.

The main advantage of using lysimeters was to relate TE to yield using the same plants, and over a long period of time. To our knowledge, this is likely the first time this has been reported. Although the data are not field data, they are collected from a system that closely mimics field conditions because: (i) plants were grown outdoors during a regular groundnut cropping season; (ii) tube size fitted well the spacing and soil depth available to peanut under field conditions; and (iii) spacing of cylinders created canopy-like conditions similar to field conditions. We assessed TE gravimetrically over almost the entire cropping cycle, therefore relating exact measurements of water uptake to plant mass, to avoid the use of surrogate traits for TE (Krishnamurthy *et al.* 2007). We argue that this field lysimetric system could be a good screening tool for TE in a large range of genotypes (on-going work).

In conclusion, variations were found in TE among the nine peanut genotypes used. Our major finding was that water uptake was critical for pod yield during a stage that corresponded broadly with the pod filling period. The genotypes differed in how much water was taken up during that stage, and this was negatively related to amount of water taken up soon after stress imposition and had a direct positive bearing on pod weight. TE also appears to be the other most important component of yield architecture and contributed approximately 30% to yield under intermittent drought. Therefore, the lysimetric system is well suited to assess different components of yield architecture.

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